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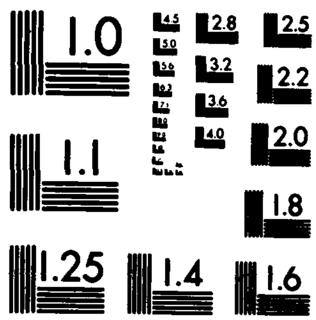

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The changes in physical and biotic environment with disturbance and subsequent recovery of arctic tussock tundra were documented. Recovery of arctic tundra disturbances may be greatly aided by stockpiling and reusing soil organic matter which contains sufficient buried seed and organically bound nutrients to revegetate many arctic disturbances. This avoids the costly process of seeding with exotic grasses which requires continuous large nutrient inputs and may delay recovery of natural tundra communities.

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REVEGETATION OF ALASKAN DISTURBED
SITES BY NATIVE TUNDRA
SPECIES

Final Report

F.S. Chapin, G.R. Shaver, and A.E. Linkins

22 September, 1982

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INTRODUCTION

This report summarizes the results of six years of research on "Revegetation of Alaskan Disturbed Sites by Native Tundra Species." The aim of the reserach was to develop methods by which the recovery of native plant populations might be promoted on development-related disturbances in northern Alaska. In contrast, current management practices depend on an expensive and massively-supported introduction of non-native grasses on disturbed sites, often with detrimental effects on native plant recovery.

The research problem is important because little is known about disturbance responses of native tundra vegetation, while development of tundra regions is proceeding rapidly. Much of the early exploration and disturbance of northern Alaska was the result of Army and other DOD activities. The widespread introduction of non-native plants into tundra regions is undesirable because they may eliminate native plants or reduce their recovery, but at the time this research began not enough was known about native tundra plants to allow their direct use in revegetation or management of disturbances.

We addressed the research problem along two principal lines. The first line of research was a series of descriptive and experimental studies of relationships between species composition, primary production, biomass turnover, and nutrient cycling in tundra ecosystems. The assumption underlying these studies was that vegetation response to tundra disturbance is largely mediated by changes in nutrient cycling caused by the disturbance. The second line of research revolved around plant population dynamics, in particular the establishment and growth of native plant seedlings in both natural and man-made disturbances. By comparing natural and man-made disturbances it might be possible to determine how well native plants might be "pre-adapted" to unnatural disturbances, and how unnatural disturbances might be manipulated to promote native plant recovery.

Species Composition, Production, and Biomass Turnover

The research on species composition, primary production, and biomass turnover began with a descriptive study of several vehicle tracks (Chapin and Shaver 1981). Soil characteristics and vegetation were studied in vehicle tracks and adjacent undisturbed tundra along local moisture gradients at four tundra sites in northern Alaska. Vehicle tracks generally had 2°C higher soil temperatures, deeper thaw, and higher concentrations of available soil phosphate than adjacent undisturbed tundra, but did not differ consistently from controls in soil bulk density, volumetric moisture content, pH, or soil organic content. Vegetation in vehicle tracks had fewer species than controls, reflecting decreased abundance of shrubs, particularly evergreens, and increased dominance by a few species of graminoids. Wet and mesic tracks exhibited a 2- to 15-fold increase in above-ground standing crop of nitrogen and phosphorus as a result of increased leaf nutrient concentrations and increased leaf biomass of graminoids, a consequence of increases in both shoot density and shoot weight. Based on these results, we rejected our original hypothesis that the known temperature effects upon root growth, nutrient absorption, and organic matter mineralization account for the increased standing crop of biomass and nutrients in vehicle trails. We concluded that other factors, perhaps related to soil water and nutrient movement, were in large part responsible for the increased nutrient status and production of vehicle tracks and exert an important control over growth in undisturbed tundra.

Results of the comparison among vehicle tracks were supported by a longer-term study on an experimentally-created bulldozed area at Eagle Creek in central Alaska (Chapin and Chapin in 1980). There succession on an organic tundra soil in interior Alaska was monitored for ten growing seasons following removal of vegetation. Exotic grasses sown following disturbance became established in the first growing season, decreased in density after 3 years and were virtually eliminated after 5 years. Fertilization did not affect initial density or long-term survival of exotic species, but did increase shoot density of native species 3 years following disturbance. Native sedges established on the disturbed site in 5-10 years, producting an above-ground biomass equal to that in undisturbed tundra. A procedure was outlined whereby the growth and reproduction of *Eriophorum vaginatum* could be manipulated by fertilization to revegetate disturbances using plants in adjacent undisturbed tundra (rather than harvested seed) as the seed source.

These two preliminary studies both supported our initial belief that plant nutrition and patterns of nutrient availability were greatly different on disturbed sites in comparison with undisturbed tundra. To simulate these differences in a controlled way, we fertilized tussock tundra at several sites, and observed the responses. Based on the preliminary studies our hypotheses were that production in tussock tundra was generally nutrient-limited, and that nutrient availability also was a major regulator of species and growth form composition. We expected that fertilization would produce: (1) higher production and biomass, (2) greater abundance of rapidly growing species with high rates of biomass turnover, and (3) greater rates of biomass turnover in the whole vegetation.

In one experiment (Shaver and Chapin 1980), the fertilization responses of six tundra species belonging to three plant growth forms were compared to test the hypothesis that species of the same plant growth form are more similar to one another than to other growth forms in their response to a controlled perturbation. The controlled perturbation was a complete factorial NPK fertilization experiment in tussock tundra at Eagle Creek, Alaska, USA. We compared deciduous shrubs, evergreen shrubs, and functionally deciduous graminoids in terms of mineral and total nonstructural carbohydrate (TNC) concentrations, and annual production per stem or tiller. Species differed in the extent to which nutrient and TNC concentrations were altered by fertilization, although concentrations were usually changed in the same direction in all species in response to a given nutrient addition. Growth forms were not consistently different from each other in the responses of nutrient and TNC concentration, and frequently the two species from the same growth form responded differently. Growth per stem or tiller was stimulated most strongly by N and/or N + P fertilization in five of six species, with small and usually insignificant differences in magnitude but not direction of the response among species. Nutrient concentrations generally responded without interaction between fertilization treatments but the growth response was usually characterized by the N*P interaction, indicating that individual nutrient concentrations may vary widely and independently but that growth at Eagle Creek requires a balanced plant nutrition with first N and then P as the prinicipal limiting factors. Decreases in TNC with fertilization suggested that carbon supply was not strongly limiting to plant growth. We concluded that species respond individually to fertilization in terms of nutrient and TNC accumulation, but that the species or growth forms studies are not distinctive from each other on the basis of limiting nutritional factors for growth. This conclusion was counter to our initial hypotheses, but we had restricted our sampling in this experiment to dominant species in undisturbed tundra only. A closer look at subdominant species (almost all rapidly-growing, high-turnover species) suggested that a change in species composition was taking place, but that the greatest changes were in least-abundant species. When we harvested the NPK-fertilized plots at Eagle Creek and other sites three years later, we found that the general prediction was confirmed.

The effects of NPK fertilization on plant community structure, primary production, and biomass were described and compared for four tussock tundra sites in central and northern Alaska (Shaver and Chapin submitted). Community responses were highly variable, although primary production and biomass were increased at all sites. Where there were large changes in relative species or growth form composition, the changes were as predicted by previous research, i.e., towards increased abundance of species and growth forms with high rates of leaf turnover. Overall species and growth form diversity was not strongly or consistently affected by fertilization.

The changes in species abundances towards increased abundance of high-turnover species were accompanied by increases in leaf turnover within species (Shaver 1981). Effects of variable mineral nutrient status on evergreen leaf longevity were investigated in the field fertilization experiment at Eagle Creek, and by comparison of plants from several sites. The species studied was Ledum palustre ssp. decumbens, with a normal leaf life expectancy of 2.06 years and a maximum leaf longevity of 4.5-5.0 yers. Most leaf losses took place during the growing season, not during the winter. Fertilization increased leaf production but decreased leaf survivorship. Total number of leaves per stem was unchanged with fertilization. In a comparison among sites, there was a moderate negative correlation between plant N and P concentrations and leaf longevity. These intraspecific responses were similar to known interspecific changes along nutrient gradients, i.e. with high nutrient availability a vegetation should become more "deciduous" and less "evergreen".

A later series of harvests revealed greater detail of the controls on evergreen leaf longevity (Shaver in press). In this research, the fertilization treatments included N alone, P along, N plus P, and N plus P plus K. After 5 years all treatments had the same effect on leaf longevity, decreasing life expectancy from about 2 years in controls to 1-1.5 years in the fertilized plants. In the NPK-fertilized plants, most of the decrease in leaf longevity was due to increased winter leaf mortality; fertilization actually decreased leaf losses during the growing season. The results are consistent with previous research suggesting that one function of overwintering evergreen leaves is to serve as nutrient storage organs, a function that is superfluous when nutrient supplies for new growth can be obtained from current uptake.

The longer-term effects of fertilization on species abundances and turnover processes suggested a reanalysis of the first fertilization experiment at Eagle Creek, using more powerful statistical methods (Lechowicz and Shaver 1982). Canonical analysis was used to analyze the results of factorial NPK fertilization trials on six species growing in arctic tundra at Eagle Creek, Alaska, USA (latitude 65°10'N, longitude 145°30'W): the graminoids Eriophorum vaginatum and Carex bigelowii, the deciduous shrubs Betula nana and Vaccinium uliginosum, and the evergreen shrubs V. vitis-idaea and Ledum palustre. In an extension of early univariate analyses, multivariate comparisons were made based on shoot concentrations of N,P,K,Ca, and Mg as a measure of overall nutrient balance. In the unfertilized controls, the graminoids were richer in K than the other growth forms, deciduous shrubs had higher concentrations of N relative to P and Ca than the evergreen shrubs, and the deciduous-evergreen contrasts were greatest early in the growing season. An NPK fertilization triggered disproportionate increases in K concentration in the graminoids and increased N relative to P and Ca in evergreen shrubs. The effect of fertilization on nutrient balance of the deciduous shrubs in the spring following fertilization was like that of the evergreen shrubs but by late summer had shifted to the graminoid pattern. Nitrogen and phosphorus consistently produced contrasting shifts in the nutrient balance in all three growth forms. In contrast to the two Vaccinium shrubs, the nutrient balance of the graminoid E. vaginatum was strongly affected by any fertilization involving potassium. In general, factorial combinations of N,P, and/or K produced shifts in the nutrient balance qualitatively intermediate to those resulting from the nutrients added singly. Many differences among growth forms apparent here were not discerned in the earlier univariate analyses of these fertilization trials. Particularly when combined with factorial fertilization experiments, canonical analysis can provide considerable insight into the response of nutrient balance to fertilization and help elucidate the ecological significance of these response patterns.

This more powerful method revealed differences in mineral nutrition among species and growth forms that were not apparent in growth responses only one year after fertilization. The work is continuing with a canonical analysis that reveals intermediate states of mineral nutrition at lower levels of fertilization, and seasonal shifts in the relative effects of N-fertilization vs. P-fertilization (Shaver and Lechowicz _in prep_.).

Recently, we expanded the scope of our research to include a study of how nutrient availability interacts with other environmental factors to control species abundances (Chapin and Shaver _in prep_.). In undisturbed arctic tussock and wet meadow tundras we increased air temperature with a plastic greenhouse, increased nutrient availability by fertilization, and decreased light intensity with shade cloth. After two years growth under these manipulations we measured growth and nutrient concentrations in each major vascular species and one moss species. Each species showed a different pattern of growth response to alteration of light, air temperature, and nutrient regimes, indicating that no single factor limits growth of all species in these communities. Growth of canopy species (_Betula nana_ and _Eriophorum vaginatum_) was reduced by experimental shading more than was growth of understory species (e.g. _Vaccinium vitis-idaea_ and _Rubus chamaemorus_). Species typical of nutrient-rich sites (_Betual nana_, _Rubus chamaemorus_, and _Polygonum bistorta_) generally responded more to nutrient addition than did species typical of nutrient-poor sites (e.g. _Empetrum nigrum_), although there were species characteristic of fertile sites (_Salix pulchra_), and infertile sites (_Ledum palustre_) which did not show this pattern of nutrient response. Species that grow in hollows between tussocks, where air temperatures may be warmer, showed less growth in response to increased air temperature than did canopy species. Leaf phosphorus concentration was greatly increased by fertilization and was generally unaffected by other treatments. Leaf nitrogen concentration increased less strongly in response to fertilization and was generally reduced (diluted over larger biomass) by treatments that caused increased growth. We conclude that the lack of single factor limitation of growth in tussock and wet meadow tundras implies (1) specialization of resource use in the communities, (2) differences in response of each species to yearly variation in weather conditions, (3) no single factor limits growth and productivity of tundra, and (4) each species in these communities is individualistically distributed, as described by the continuum model of community organization.

Finally, we have used factorial NPK fertilization experiments to compare limiting factors among several tundra sites (Shaver and Chapin _in prep_.). The two tussock sites (Eagle Creek and Toolik Lake) both showed a strong N-limitation of _Eriophorum_ production, but at Eagle Creek there was also a strong N*P interaction. The two wet sites differed greatly: at Atiqun Gorge production was strongly and exclusively N-limited while the principal limiting nutrient at Franklin Bluffs was P. These results suggest that it is difficult to generalize about specific nutrients as limiting factors even within a tundra vegetation type although, overall, tundra production is strongly nutrient-limited.

Nutrient Cycling

The importance of nutrient availability to production and abundance of native tundra plants led us to more detailed studies of nutrient cycling processes. This research is not as advanced, but it is continuing under the current 3-year extension of the research.

In a study of decomposition processes in disturbed and undisturbed tundra, *Eriophorum* litter from plants growing in or out of vehicle tracks was placed in litter bags which were set out in and out of the tracks in a reciprocal experimental design. The question asked was whether the conditions under which a litter was produced were more or less important than the soil environment in which a litter decomposed. Decomposition characteristics of interest were total weight loss and the time course of N and P immobilization and later release. Results after two years show that by far the greatest effect was that of soil environment, in particular the effect of moving soil water. There was no significant difference in decomposition of any litter type in or out of a mesic track, but the same litter placed in wet tundra showed higher N and P immobilization, and in a wet track with surface water movement the amounts of N or P immobilized were 6-8 times that of litter placed in either mesic site. These results confirm the importance of soil water as having a major impact on nutrient movement in tundra soils, and thus nutrient availability to decomposers or (presumably) to plants.

Soil water may strongly influence nutrient availability in vehicle tracks through its effect on soil oxygen. Under conditions of low soil oxygen, iron would be converted from ferric to the ferrous oxidation state. Ferrous phosphate is much more soluble than ferric phosphate, so reduced soil oxygen in a vehicle track might render phosphate more available. So far there is conflicting evidence for this idea. Bulk soil from vehicle tracks has a redox potential that should generate ferric iron (our unpublished data) while relatively high soil oxygen concentrations have been measured. However, the oxygen diffusion rate is slow in tundra soils, so anaerobic areas (with higher phosphate availability) may very well exist in track soils.

Soil oxygen and temperature will also influence the source and dynamics of phosphorus in these soil systems, because soil phosphatases are inhibited by solution inorganic phosphorus. Anaerobic soil conditions with attendant increases in soluble ferrous phosphate should inhibit phosphatase activity in the soils, on mycorrhizal and nonmycorrhizal roots. Anaerobic conditions are expected to exist in the soils during the winter, because soils begin freezing from the surface downward (decreasing the rate of oxygen supply to soil) while decomposition continues in thawed soils at substantial rates and depletes soil oxygen. Phosphatase-temperature curves suggest that 11-18% of the total annual organic phosphorus mineralization could occur during winter (between -10° to 25°C). The inhibition of phosphatase by accumulation of inorganic ferrous phosphorus may be an important factor in determing annual phosphorus dynamics.

Analysis of the extracellular soil enzymes phosphatase and cellulase has been completed from vehicle track and control soils at Materials Site 119 on the Haul Road. Soil samples were collected from both wet (soil moisture 460% dry wt) and mesic (soil moisture 40% dry wt) areas in July 1979.

1) Phosphatase activity: Wet-site control soils had 40% greater activity than the vehicle track soils at the same site. Activity in these wet control soils was 20-30 fold greater than in either the mesic control or the mesic track soils, respectively.

The optimum pH of phosphatase activity was 5.0 for all soils. Measured in the field, soil pH was: wet control, 5.8; wet track, 5.2; mesic control, 4.7; mesic trail, 4.7.

2) Cellulase activity: Cellulase activity as both the endo- and exo-glucanase component was determined in both wet and mesic track and control soils. Temperature response curves for both enzyme groups were constructed over the temperature range 0-65°C. Critical statistical analysis was conducted over the 0-20°C range because that is the range or normal summer soil temperatures.

In the wet site soils both endo- and exo-glucanase activities were 53% higher in the track than in control soils. Activity within the 0-20°C range showed a 27% steeper slope in the temperature response curve for track soils vs. controls. Mesic soils generally had 85-90% lower cellulase activities than the wet soils. Within the mesic site, track soils had 26% greater cellulase activity than control soils. Temperature response curves for the mesic track soils were 30% steeper in slope than for the mesic control soils. Functional comparison of the nature of cellulose hydrolysis in the four soil types (i.e. endo:exo ratio consistently was 0.25-0.22, suggesting no significant difference in the nature of hydrolysis among these soils.

Plant Population Dynamics

Variation in nutrient availability are meaningless in the context of this research if the native plants are not present in disturbances. Establishment of native plant populations depends upon a seed source, adequate conditions for germination, and survival of seedlings to produce a mature native plant community. To understand controls on native plant establishment, we studied a number of stages in the plant life cycle, focusing on one species, *Eriophorum vaginatum* L., because it is dominant both in undisturbed tussock tundra and in a wide variety of natural and construction-related disturbances.

We began with a study of production and "reproductive effort in undistrubed tussock tundra" (Chester and Shaver 1982). The hypothesis tested in this research was that the success of *E. vaginatum* on disturbed sites might be achieved through a higher allocation of biomass to reporductive structures relative to other tundra species. Reproductive allocation of tundra plants in general also was compared with plants of the temperate zone. The results indicate that E. vaginatum is about average among the common tundra species in terms of total reproductive allocation, allocation to seeds, and the proportion of total reproductive allocation that is accounted for by viable seeds. Tundra species, on a relative basis, allocate less biomass to all reproductive structures than temperate species but not necessarily less biomass to the output of viable seeds. Both in this study and later research by Gartner (1982) it was shown that current seed production was insufficient to account for all of the seedlings that appeared in disturbed sites.

Subsequently, McGraw (1980) showed that an additional, perhaps very important seed source was available as buried seed in undisturbed tundra soils. Soil from cottongrass (Eriophorum vaginatum) tussock tundra at Eagle Creek, Alaska, was analyzed with respect to the distribution, abundance, and germination patterns of buried viable seeds. Seeds of Carex bigelowii, Eriophorum vaginatum, and Ledum palustre were abundant. Smaller ammounts of Empetrum nigrum and Betula spp. were also present. Buried seeds were found to 21 cm below the soil surface. Germination was rapid in the first 3 weeks of exposure to greenhouse conditions and continued at a slower rate for 5 more weeks. The ecological importance of seed banks in arctic regions and their possible implications for management of cottongrass tussock tundra vegetation were discussed. Gartner (1982) found similar large seed reserves in the soils near Toolik Lake, and additionally noted that there was a characteristic horizontal as well as vertical seed distribution pattern.

It has never been certain to what extent arctic plants depend on seed reproduction in undisturbed tundra. Previous workers have suggested that reproduction by seedling establishment is less important in the maintenance of tundra vegetation than in temperate areas, but few quantitative data are available. In a survey by McGraw and Shaver (1982), seedling densities were studied at 11 tundra sites in or near disturbed and undisturbed cottongrass tussock tundra in Alaska, and numerous seedlings were found. Examination of seedling age structures suggests that at least Ledum palustre and probably also Empetrum nigrum do replace themselves by seed in undisturbed tundra. Seedling densities vary greatly depending on the substrate available for establishment. Gartner (1982) continued these observations and found seedlings in greatest numbers on or near natural disturbances such as frost boils. She found that extremely active frost boils would not support seedlings but that the greatest germination rates occured and the largest seedlings were found on natural disturbances that had been stabilized by growth of hepatics or mosses.

On artificial disturbances, the dynamics of seedling establishment, and growth of native cottongrass-tussock tundra species were studies during the natural revegetation of small bare areas excavated in tussock tundra (Chester and Shaver 1982b). The seedlings of Eriophorum vaginatum spp. spissum and Carex bigelowii, two sedge species, established most successfully. Few seedlings of nonsedge species emerged with the small disturbances. Most seedling emergence, occurred early in the first growing season following the excavation of the bare areas, before any seeds were shed in surrounding undisturbed tundra. This suggested that buried seed were an important seed source in revegetation. The density of emerged seedlings was higher in bare areas excavated in the autumn preceding the observations, rather than in bare areas excavated at the start of the first season of observation. After two growing seasons, survival of seedlings was not affected by the time the seedling emerged within the growing season. Eriophorum vaginatum was the most abundant species because it: (1) had the highest seedling emergence rates, particularly early in the growing season; (2) produced more tillers per seedlings; and (3) had a higher growth rate per seedling than C. bilelowii. In a more extensive analysis of controls on revegetation of disturbances by native plant species, Gartner et al. (in prep.) found that presence or absence of buried seed was the major factor governing natural revegetation of a bulldozed disturbance in Alaskan tussock tundra. The germinable buried seed pool contained 97% Eriophorum vaginatum and Carex bigelowii seed and was restricted to organic soil horizons. Consequently, disturbed organic soils reached a final seedling density of 250 seedlings m^{-2} (primarily Carex and Eriophorum) four years after disturbances, whereas mineral soils which were colonized by current seed rain had only 30 seedlings m^{-2}, including many grasses. Fertilization enhanced the growth of grass and 2- to 4-yr-old Carex seedlings 4- to 10-fold but had no significant effect upon Eriophorum seedling growth. Growth was not significantly affected by presence of already established seedlings and did not differ between substrates except for grasses which grew more rapidly on mineral than organic soils. Seedling mortality during the first 2 years after germination was low (41% in Eriophorum, 27% in grass, and 14% in Carex) and did not differ between organic and mineral substrates. Mortality of 1- and 2-yr-old seedlings was concentrated during the growing season, but mortality of larger seedlings was primarily a consequence of winter herbivory. Mortality was increased by fertilization. The greater vascular plant biomass and cover on organic than mineral soils was due primarily to recruitment from the buried seed pool. The increase in biomass and cover with fertilization was a consequence of a stimulation of growth by grass and Carex.

Beyond the seedling stage, different factors were found to regulate native plant growth on disturbed vs. undisturbed sites (Fetcher and Shaver 1982). Growth patterns were investigated for Eriophorum vaginatum tussocks from disturbed and undisturbed tussock tundra at two sites in Alaska. Total basal area of tussocks decreased with increased cryoturbation but mean basal area per tussock did not. Flowering was observed in tussocks of significantly smaller size on disturbed compared to undisturbed tundra. For tussocks with less than 10% cover by shrubs and moss, number of tillers per tussock was linearly related to tussock diameter in most disburbed and undisturbed sites. Exceptions occurred in an area that had been bladed with a bulldozer 7 years before our survey where tiller number increased as the square of diameter and in an area with much frost activity where tiller number was not correlated with diameter. The ratio of daughter tillers to adult tillers decreased with diameter in disturbed tundra, whereas the trend was less pronounced in undisturbed tundra. Microsuccession in undisturbed tussock tundra was investigated by sampling tussocks with different amounts of shrub and moss cover for number of daughter tillers per adult tiller, weight per tiller, percent nitrogen, and percent phosphorus. Small tussocks without cover by other species and large, partially covered tussocks were not significantly diffferent by any measures, but tussocks that were almost completely buried had significantly (p less than 0.05) lower values of tillering index, weight per tiller, and percent phosphorus.

The work by Fetcher and Shaver (1982) showed that growth relationships differed greatly in Eriophorum on disturbed vs. undisturbed sites. In a more quantitative approach, the demography of Eriophorum tillers was studied by Fetcher and Shaver (in press). Life tables were constructed for vegetative tillers of Eriophorum vaginatum from undisturbed and disturbed tussock tundra in Alaska. Life tables were also constructed for tillers from tundra that had been fertilized with N,P, and K. The life tables were used to estimate population parameters and to construct constant coefficient matrix models of tiller demography. Tiller survival was lower in disturbed than it was in undisturbed tundra, and daughter tillers were produced sooner. Addition of nutrients (as mineral fertilizer) produced no change in tiller survival and in the age distribution of daughter tiller production in the first year following fertilization. The shapes of the survival curves were intermediate between Deevey Type I and Deevey Type II curves. The generation time for tillers in undisturbed tundra was 5.3 years, about twice as long as in disturbed tundra while the annual rate of increase of tillers did not differ greatly. Fertilization produced large increases in the annual rate of increase, but the generation time was shortened only slightly. Reproductive values, defined as the expected number of daughter tillers from tillers of a given age relative to the expected number from a tiller aged 0, fell into one of three patterns: (i) decline from maximum value at age 0; (ii) increase from age 0 followed by a monotonic decline; (iii) increase from age 0 followed by a gradual, irregular decline and a plateau in the older age classes. The peak in reproductive value for patterns (ii) and (iii) occurred 2-4 years after the onset of tillering at age 1 or 2 years; this result was attributed to increases in age-specific tillering rate with tiller age. Sensitivity analysis of the matrix models revealed that sensitivity of the annual rate of increase to changes in tillering rate and survival declines with age. The annual rate of increase was equally sensitive to changes in tillering rate and survival from age 0 to age 3. In the older age classes the annual rate of increase was more sensitive to changes in tillering rate than to changes in survival.

The general conclusion of the Fetcher and Shaver studies was that Eriophorum is so successful on both disturbed and undisturbed sites at least in part because it is capable of responding to different environments by varying its tiller life histories. In a theoretical paper, Fetcher (submitted) addressed the question of the "optimality" of Eriophorum life histories.

Two independent models for optimal life histories were used to predict attributes of the demography of tillering of Eriophorum vaginatum growing at two sites in Alaska. The first model predicted the optimal age of first production of daughter tillers, where the optimum is defined as the age of first tillering that maximizes the rate of population growth when the population is in the stable age distribution. The predicted age was 4.33 years. The observed distribution of ages at which daughter tillers were produced had a peak at 4 years. Because most tillers of E. vaginatum less than 5 years old are producing daughters for the first time, the results appear to support the model. Survival costs of tillering were estimated by dividing the change in age-specific survival rate by the change in age-specific tillering rate. The second model predicted that such costs would increase with age. This prediction was supported also. Thus, tillers of E. vaginatum may possess optimal life histories, where the optimum is reached when the rate of growth of the tiller population in the stable age distribution is maximized.

Additional Research

The research on disturbance and native plant recovery also afforded an opportunity to continue ongoing research in tundra ecology. This work was not directly related to the main research problem, but it produced important results.

In the first study (Shaver, Chapin, and Billings 1979), growth and nutrient relations of Carex aquatilis were examined in the field and in glasshouse-grown plants from five polygon microhabitats in wet meadow tundra at Barrow, Alaska. These habitats can occur within 1 m of each other, and differ greatly in soil moisture, availability of N and P and thaw depth. Field-grown plants from these microhabitats differed between populations in above-ground weight per tiller, leaf-production rate, root:leaf weight ratio, rate of uptake of ^{32}P, and concentration of sugar, N and P in roots and rhizomes. Tissue concentrations of N and P were correlated with corresponding availability in the soil but not with plant size. There was a moderate positive correlation between soil moisture and plant size. Carex aquatilis populations grown in the glasshouse with either addition or moderate addition of phosphate showed no significant differences in plant size, but large differences in tissue-nutrient concentrations, ^{32}P-uptake kinetics and responsiveness to phosphorus availability. A strong effect of phosphorus stress on nitrogen and potassium metabolism was observed. Responsiveness of ^{32}P-uptake kinetics to changed conditions was inversely related to the degree of responsiveness in growth rate and mineral accumulation in the tissues. These ecotypic differences among populations of Carex aquatilis are remarkable in view of the extreme rarity of reproduction by seed in the field, and the close proximity of the populations. The differences suggest a strong degree of selection among genotypes, probably by differential growth of clones in a period of polygon development in old, drained lake basins.

A second study continued the research on ice-wedge polygon communities (Shaver submitted). The question addressed in this research was, "If two sites are similar in community composition, can one say that they are also similar in plant mineral nutrient status and plant size?" Patterns of similarity in community composition, concentration of N,P,K,Ca, and Mg in leaves, and leaf weight per tiller of the dominant graminoid species were compared for eight sites in polygonal wet tundra at Barrow, Alaska. Four of the sites represented variation within one microhabitat type, the wet meadow. The other four represented four other microhabitats. Within-species similarities and differences in element concentrations followed a patterns very different from the pattern of variation in community composition among sites. Three species showed similar changes in element concentrations from site to site, but different correlations between leaf weight and concentration of specific elements. This contrast in the behavior of individual species vs. whole communities suggests that the environment to which an individual species responds is more variable than one would predict from patterns of community composition. Community composition differs from site to site as a result of differential effects on growth, not on element concentration.

Finally, we have summarized the basic knowledge gained over the years of our research in a review paper on the physiological ecology of arctic plants (Chapin and Shaver in press). This paper integrates our results with the research of numerous other workers over the past 20 years.

Summary and Management Recommendations

Results of this research are summarized in a series of management recommendations (Gartner 1982, Gartner et al. in prep, Chapin et al. *in prep*.). Based on what we have learned, it appears that our original plan (to increase seed production adjacent to disturbances) will not work because most native plant populations are established in disturbances from buried seed. Our recommendations now are to stockpile and reuse soil organic matter as a ground cover, supplemented under certain conditions such as severe erosion potential by fertilization and/or sowing of non-native plants. These methods may be slower to establish complete ground cover, but they will increase recovery of native plants over present methods, at lower cost.

DEGREES AWARDED

Chester, A.L.	M.S. Degree San Diego State University. 1979
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Herbein, S.A.	M.S. Degree Virginia Polytechnic Inst. & State University. 1981
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PUBLICATIONS AND REPORTS

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